

# The last dicynodont: an Australian Cretaceous relict

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Some long-forgotten fossil evidence reveals that a dicynodont (mammal-like reptile of the infraorder Dicynodontia) inhabited Australia as recently as the Early Cretaceous, *ca.* 110 Myr after the supposed extinction of dicynodonts in the Late Triassic. This remarkably late occurrence more than doubles the known duration of dicynodont history (from *ca.* 63 Myr to *ca.* 170 Myr) and betrays the profound impact of geographical isolation on Australian terrestrial faunas through the Mesozoic. Australia's late-surviving dicynodont may be envisaged as a counterpart of the ceratopians (horned dinosaurs) in Cretaceous tetrapod faunas of Asia and North America.

**Keywords:** dicynodonts; Cretaceous; biostratigraphy; biogeography; extinction

## 1. INTRODUCTION

Dicynodonts were bizarre herbivorous therapsids (mammal-like reptiles) that flourished worldwide during the Permian and Triassic periods (Hotton 1986; King 1990; Angielczyk 2001; Rubidge & Sidor 2001). In their general appearance and habits dicynodonts probably resembled pigs or small hippopotamuses, though their teeth were largely replaced by a massive horny beak like that of a turtle. Most retained only a single pair of teeth, in the form of large maxillary tusks. Dicynodonts survived the biotic turnover defining the Permian–Triassic boundary but eventually succumbed to extinction in the Late Triassic: the last known dicynodonts are often dated as Late Carnian (*ca.* 222 Myr ago), although some may have lingered into the Norian (*ca.* 215 Myr ago (Lucas 1995)).

Here we present some long-overlooked fossil evidence showing that dicynodonts survived in Australia until the Early Cretaceous (Albian, *ca.* 105 Myr ago)—more than 100 Myr after their supposed extinction. This remarkably late occurrence more than doubles the known duration of dicynodont history, from *ca.* 63 Myr to *ca.* 170 Myr. It is also an example of a Lazarus taxon even more impressive than the extant coelacanth *Latimeria*, which was discovered only *ca.* 65 Myr after the supposed Late Cretaceous extinction of crossopterygian fishes.

## 2. MATERIAL

The evidence comprises six fragments of fossil bone, registered at the Queensland Museum, Brisbane, in June 1915 (specimen QM F15.990). These had been collected the previous year from an erosion gully in sediments of the Rolling Downs Group (Early Cretaceous, Aptian–Albian) on Alderley station, about 32 km west of Hughenden in north-central Queensland (figure 1). Adherent matrix, a yellowish-brown mudstone, betrays their most likely source as the Allaru Formation, a thick (*ca.* 250 m) succession of mudstones and siltstones which outcrop

extensively in the region of Alderley (Vine 1970). The material is unlikely to have originated from the limestones of the underlying Toolebuc Formation, which is extremely thin or absent in the Alderley area, or from the still deeper-lying Wallumbilla Formation, which is rarely exposed and often glauconitic or carbonaceous. The bones show no indication of protracted transport or reworking and their preservation is identical to that of other tetrapods from the Rolling Downs Group, including turtles, ichthyosaurs, plesiosaurs and dinosaurs (Molnar 1991, 1996*a,b*; Wade 1990; Thulborn & Turner 1993). There are no outcrops of pre-Cretaceous rocks in the vicinity of Alderley (Vine 1970), and the Rolling Downs Group is overlain disconformably by basalts of Late Tertiary to Early Quaternary age.

Sediments of the Allaru and Toolebuc Formations accumulated in a shallow epicontinental sea and are dated as Early Cretaceous (Albian) on the basis of their rich and varied marine biota, which includes foraminiferans, bivalves, gastropods, nautiloids, belemnites, ammonites, fishes and marine reptiles (see Dettmann *et al.* 1992; Burger & Shafik 1996; Henderson *et al.* 2000). The Alderley dicynodont was probably introduced into that marine environment as a stray carcass derived from an adjoining land-area, as were various dinosaurs.

The most informative fragment is a left maxilla containing the stump of a large tusk (figure 2). In July 1915 this specimen was exhibited at a meeting of The Royal Society of Queensland, where Heber Albert Longman, then Assistant Director of the Queensland Museum, introduced it as 'an animal quite new to Australia' in which 'some slight resemblance might be traced to the Dicynodonts of South Africa' (Anon. 1915). This was a prudent and perceptive appraisal. Longman had no comparative material and at that date the cranial anatomy of dicynodonts was imperfectly known. Moreover, there was no independent evidence of dicynodonts (or, indeed, of any mammal-like reptiles) in Australia: the first example of an Australian dicynodont was reported barely 20 years ago, from the Lower Triassic of Queensland (Thulborn 1983). Also, most significantly, the Alderley fossils were divorced

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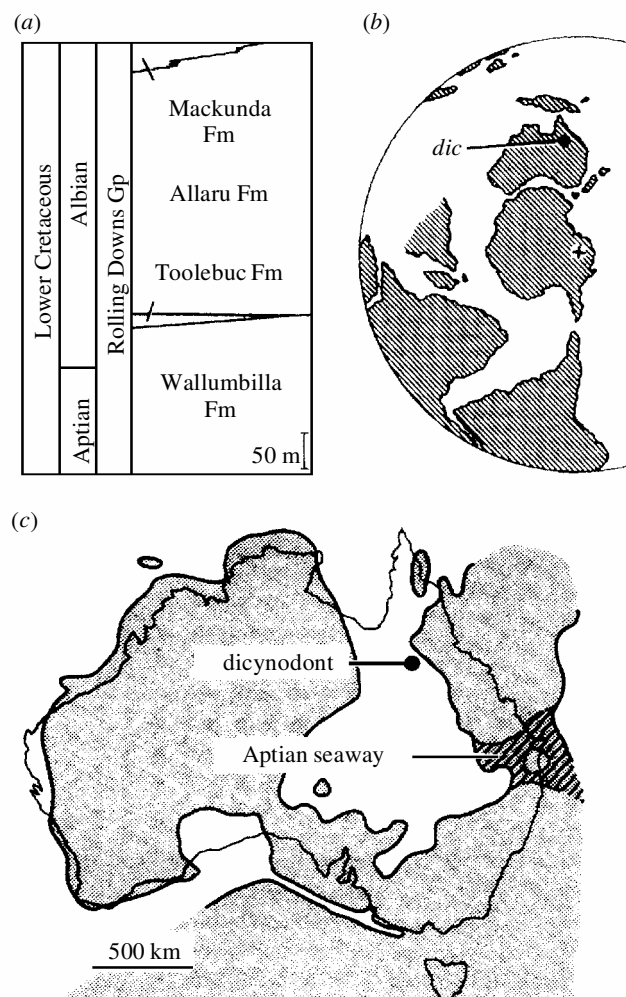


Figure 1. Stratigraphic and geographical context of the Australian Cretaceous dicynodont QM F15.990. (a) Stratigraphic relationships of sedimentary rock units outcropping to the west of Hughenden, north-central Queensland (after Vine 1970; Vine & Paine 1974). (b) South polar projection showing disposition of Gondwana continents in the Early Cretaceous (Albian *ca.* 105 Myr ago); source of dicynodont remains (*dic*) is geographically remote, with high-latitude trans-Antarctic connection to other Gondwana continents. (c) Palaeogeography of Australia in Middle and Late Albian, with land areas indicated by even shading; dicynodont remains probably originated from the land area immediately to the east (Queensland Plateau), which previously had been isolated by a seaway (oblique shading) during the Aptian marine transgression. Maps adapted from Dettmann *et al.* (1992) and Henderson *et al.* (2000).

from even the latest known dicynodonts by an enormous interval of time, now estimated at *ca.* 110 Myr (Young & Laurie 1996). However, despite its potential importance, the material from Alderley was never described or illustrated, and its existence has been overlooked up to the present day.

### 3. DESCRIPTION

The maxilla (figure 2) is a thick slab of bone with a flat medial face and an outwardly arched lateral face. In lateral view it is roughly triangular, with the ventral margin extended into a caniniform process that encloses the root

of the tusk. As the rear wall of the caniniform process is not preserved, the presence or absence of a labial fossa cannot be ascertained. In front of the tusk the thin occlusal margin slopes upwards towards the premaxilla. During life this thin and toothless jaw margin was probably sheathed in keratin to form a robust beak. Above the tusk the lateral face of the maxilla sweeps upwards, outwards and backwards to form the anterior root of the exaggerated zygomatic arch that is characteristic of the dicynodont skull. A short section of the narial margin is preserved intact; as there is no definite trace of the septomaxilla, the narial shelf seems likely to have comprised only maxilla and premaxilla. Between the naris and the jaw margin the external face of the maxilla is slightly bevelled where it was overlapped for a short distance by the subnarial ramus of the premaxilla. A deep elliptical pocket in the anterolateral face of the maxilla is an unusual feature that occurs only sporadically among the dicynodonts, seemingly as an individual variation (see below). Its floor is sufficiently deep to expose the root of the tusk, and a shallow notch in its upper margin leads into a faint groove extending anterodorsally towards the rim of the external naris.

On its medial side the maxilla is dominated by a large, steep and slightly wrinkled surface for the attachment of the massive premaxilla, above which is the deep and rather smooth lateral wall of the nasal passage. The floor of the nasolacrimal duct is represented by a narrow gutter extending backwards and then slightly upwards towards the anterior wall of the orbit.

As in other dicynodonts, the maxilla makes only a limited contribution to the highly vaulted palate, merely a narrow strip alongside the jaw margin. This palatal surface is marked with faint dimples betraying the extensive attachment of keratinous tissue. At its posterior end the maxilla expands medially, towards the palatine, and bears a sliver-like fragment of a single postcanine tooth. This tooth does not lie directly behind the canine tusk but is displaced medially, like the postcanines in other dicynodonts.

The tusk is slightly recurved, open-rooted (*i.e.* continuously growing) and has a rounded triangular outline in cross-section, being slightly flattened on the external face and very weakly concave at the rear. Its root is covered by a film of rough cement-like tissue similar to that described in *Dicynodon* (Owen 1845) and *Placerias* (Camp & Welles 1956). The crown of the tusk lacks enamel and internally it exhibits the typical dicynodont pattern of concentric banding. Closer inspection reveals that the bands of dentine form a stack of nested cones, a structural pattern seemingly unique to dicynodonts (see Camp & Welles 1956; Cox 1968). The tip of the tusk is wedge-shaped, displaying a pattern of abrasion typical of dicynodonts (Pearson 1924b; Cox 1968; Cruickshank 1978): a distinct facet on the medial side resulted from wear against the horny beak of the mandible, whereas the external surface was probably abraded during foraging or digging.

The left nasal (figure 4a) is a thick sheet of bone with a roughly trapezoidal outline. It is very similar to the nasal in a skull attributed by Seeley (1889) to *Dicynodon tigriceps* (*D. lacerticeps?*), though its anterolateral corner is slightly more acute and swells into a small tuberosity above the external naris, as in *D. leoniceps* of Owen (1876) (*D. lacerticeps?*) and some dicynodonts of the family Kanne-

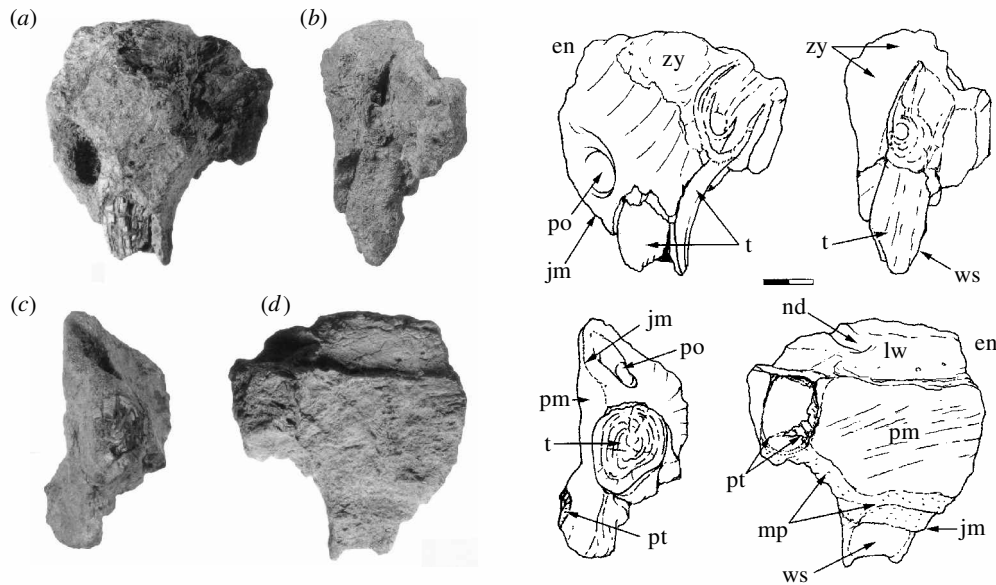


Figure 2. Left maxilla of the Cretaceous dicynodont QM F15.990 in (a) lateral, (b) posterior, (c) palatal and (d) medial views. Scale bar, 2 cm. en, rim of external naris; jm, thin and sharp-edged margin of jaw; lw, smooth lateral wall of nasal passage; mp, pitted palatal surface of maxilla; nd, smooth channel representing floor of nasolacrimal duct; pm, large corrugated scar of attachment for premaxilla; po, deep pocket in anterolateral face of maxilla; pt, postcanine tooth; t, large open-rooted tusk; ws, worn medial surface of tusk, abraded by contact with horny bill of mandible; zy, broken anterior root of zygomatic arch.

meyeriidae (Renaut & Hancox 2001). Its medial edge is thickened in characteristic dicynodont fashion (Watson 1948) and formed a weak median ridge on the snout—sometimes regarded as a distinctive feature of the kannemeyeriids (see, for example, Pearson 1924a; Cox 1991; Renaut & Hancox 2001).

The remaining four fragments are not so easy to interpret. Two of them represent short segments of a stout girder-like structure with polygonal cross-section; these are probably parts of the exaggerated zygomatic arch that is typical of dicynodonts (figure 4a). A small splinter-like fragment with a thick corrugated edge may represent part of the orbital rim, either the frontal or prefrontal. Finally, a small and featureless piece of sheet-like bone, only a few millimetres across, is of uncertain identity. It might perhaps have originated from the ethmoid region, in proximity to the more securely identified fragments.

In summary, the several fragments found with the left maxilla are readily attributed to the left facial region of a single dicynodont skull (figure 4a), though they have no diagnostic dicynodont features and their anatomical positions are determined only approximately. The intact skull would have been *ca.* 40 cm long, assuming the tusk-bearing part of the maxilla to represent about one-quarter of skull length, as in most other dicynodonts.

#### 4. DISCUSSION

The discovery that dicynodonts survived into the Early Cretaceous is so extraordinary that it demands exceptionally rigorous investigation. Does the fossil material from Alderley really represent a dicynodont, and is it really Cretaceous in age?

##### (a) *A dicynodont?*

Every anatomical feature in the Alderley material occurs widely or universally among dicynodonts (e.g. reduction

of septomaxilla, loss of teeth from anterior part of maxilla, restricted maxillary contribution to palate, medial migration of postcanine teeth, vaulted secondary palate, etc. (see King 1990, pp. 219–225)). Some of the correspondences are very striking. For instance, the detailed cross-sectional shape of the tusk is identical to that in Owen's illustration of *Dicynodon leoniceps* (Owen 1876, pl. 24, 26): in both cases the outline is roughly elliptical but tending to triangular, with slight flattening on the external face and at the rear. Even the pattern of fractures affecting the Alderley maxilla is matched in a large *Dicynodon* skull illustrated by Owen (1876, pl. 38 (*D. pardiceps*)).

Several features are diagnostic for dicynodonts. The occlusal margin of the maxilla is developed into a canini-form process (Angielczyk 2001), and the narial shelf seems to have been composed entirely of maxilla and premaxilla, with no contribution from the palatine (Modesto *et al.* 1999). The tusk shows the characteristic dicynodont pattern of tooth wear and appears to have been open-rooted, with a deep conical cavity in its base. The base of the tusk is preserved with a cross-section of narrow elliptical outline, having collapsed in response to crushing, but if it were restored to more nearly circular cross-section, like the solid distal parts of the tusk, it would necessarily have to contain a large conical cavity. That cavity would match the 'conical excavation' that Owen (1845) described and illustrated as a diagnostic feature of *Dicynodon*. Finally, the tusk lacks enamel and its dentine layers are arranged as a stack of nested cones, a pattern of tooth structure seemingly unique to dicynodonts (see, for example, Camp & Welles 1956; Cox 1968). At its broken distal end the tusk reveals concentric banding of the dentine, which is the pattern normally seen in transverse section of dicynodont tusks and is consistent with cone-in-cone structure (e.g. Owen 1845, pl. 5; 1876, pl. 38; Cox 1968, p. 14; Cluver 1971, p. 189). The proximal end of the tusk, exposed within its broken alveolus, shows remnants of at



Figure 3. Structure of maxillary tusk in the Cretaceous dicynodont QM F15.990. Longitudinal section (CAT scan) showing alternating light and dark bands arranged in a herring-bone pattern (i.e. as nested cones, with apices directed distally); some fractures (bright lines) coincide with interfaces between cones of dentine. Scale bar, 1 cm.

least three nested cones, very like those in the base of a *Dinodontosaurus* tusk illustrated by Cox (1968, figs 10D,E). Although longitudinal sections (computer aided tomography (CAT) scans) of the tusk are obscured by fracturing they do nevertheless exhibit alternating light and dark stripes arranged in a herring-bone pattern (i.e. in nested cones; figure 3). Some of the fractures traversing the tusk developed along, and highlighted, the interfaces between successive cones of dentine, so that the overall pattern of banding and fractures resembles that illustrated by Cox (1968) in a tusk of *Dinodontosaurus*. Every aspect of the tusk, whether external or internal (CAT scan), reveals indications of cone-in-cone structure.

Although the Alderley material matches dicynodonts in every significant respect, it does not resemble any other group of tetrapods in even a single important feature—aside from thecodont tooth implantation, which is widespread and is matched in dicynodonts anyway. The maxilla cannot be attributed to any group of tetrapods known to occur in the Rolling Downs Group or, in fact, to any group of tetrapods known to exist in the Jurassic or Cretaceous. We have investigated every conceivable identification for the Alderley maxilla: it is not dinosaurian or crocodilian, or plesiosaurian (either elasmosaur or pliosaur); it is not from a turtle (edentulous) or an ichthyosaur (with labyrinthodont teeth and pleurodont implantation); neither is it referable to any of the sharks or teleost fishes which are common in the Rolling Downs Group and sometimes attain very great size (see, for example, Turner & Rozefelds 1992). Nor is it referable to the temnospondyls—a labyrinthodont ‘amphibian’ group that survived into the Early Cretaceous in Australia (Warren *et al.* 1991, 1997): temnospondyls have broad

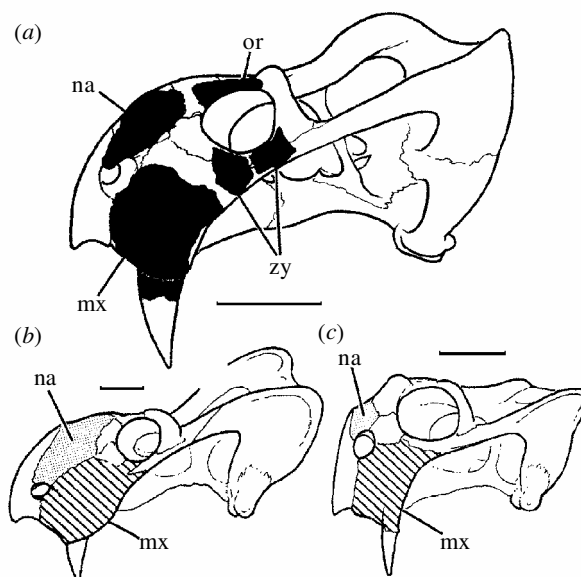


Figure 4. (a) Outline of generalized dicynodont skull in left lateral view, showing approximate anatomical relationships of five skull fragments from the Cretaceous of Queensland, specimen QM F15.990. A sixth fragment (not shown) is very small, featureless and of uncertain anatomical relationships. (b,c) Skulls of the common Triassic dicynodonts *Kannemeyeria* (b) and *Lystrosaurus* (c), showing differences in size and shape of the maxilla and nasal; in the proportions of these bones the Queensland dicynodont is closer to *Kannemeyeria* than to *Lystrosaurus*. mx, maxilla; na, nasal; or, orbital rim; zy, suborbital portion of zygomatic arch. Scale bar, 10 cm. Skull outlines adapted from Cluver (1971) and Brink (1982–1988).

flat, almost crocodile-like skulls with elaborate ornament and close-packed labyrinthodont teeth, whereas the Alderley maxilla is clearly from a deep-snouted animal, with weak skull ornament and a solitary tusk that lacks enamel (let alone infolded enamel). We must also discount the possibility that the Alderley material might represent some megafaunal element derived from alluvial deposits of Tertiary or Quaternary age: it clearly does not represent the giant lizard *Megalania* or the giant snake *Wonambi*, or any of the big marsupials such as *Diprotodon* or *Thylacoleo*. The only identification supported by positive evidence, in the form of demonstrable similarities and diagnostic features, is ‘dicynodont’.

No Jurassic or Cretaceous tetrapods rivalled dicynodonts in reducing the marginal dentition to a single pair of maxillary tusks. There are no sabre-toothed turtles, crocodiles or plesiosaurs. The only tusk-bearing dinosaurs are the African heterodontosaurids (ornithischian family Heterodontosauridae), and these differ in being much smaller and earlier (Triassic–Jurassic boundary) and in having rows of elaborately ridged cheek teeth as well as tusks in both upper and lower jaws (Crompton & Charig 1962). Beyond that, the tusks of heterodontosaurids differ from those of dicynodonts in being fully enamelled and blade-like, with ridged and serrated margins.

On the positive side, our identification of the Alderley material as ‘dicynodont’ fits very neatly with current understanding of dicynodont phylogeny. This late survivor finds its closest match among members of the most widely

distributed and longest-enduring clade of dicynodonts, a group that included the genera *Dicynodon*, *Lystrosaurus* and *Kannemeyeria* (Angielczyk 2001; Maisch 2002) and that is known to have inhabited Australia during the Triassic (King & Thulborn 1983; Thulborn 1983). Furthermore, the late survival of a dicynodont in Australia is consistent with what is known already of the geographical isolation and faunal peculiarities of East Gondwana during the Mesozoic (examined below).

In summary, all available evidence supports identification of the Alderley material as a late-surviving dicynodont, and we are unable to find even a single feature that would weaken or contradict that identification. If the Alderley material had originated from Permian or Triassic rocks it would probably be accepted without hesitation as a perfectly ordinary dicynodont. That response greeted the first dicynodont specimens from Antarctica, isolated maxillae which, in nearly every respect, are anatomically equivalent to the example we describe here. One of those maxillae was assigned to the well-known genus *Lystrosaurus* (Colbert 1974) and the other to the equally well-known *Kannemeyeria* (Hammer *et al.* 1990), despite their unprecedented source in Antarctica. The maxilla from Alderley is comparable evidence for the existence of a dicynodont in Australia.

#### (b) Cretaceous age?

Specimen QM F15.990 was delivered to the Queensland Museum in May 1915, along with a batch of other fossils (ammonites, belemnites, bivalves, fish vertebrae, turtle and ichthyosaur fragments) that were all quite unremarkable and typical of the Rolling Downs Group. All these specimens (QM F15.986–QM F15.991) had been collected on Alderley station by Frederick L. Berney, one of Longman's notable collectors (Turner & Wade 1986), with some assistance from the landowner, Robert Pool. Pool's letter to the Queensland Museum (dated 15 May 1915) explained that QM F15.990 was discovered 'five feet lower down the gully in which the other fossil was found; all these fossils were found in gullies washed out from under the basalt near the Flinders River'. The basalt overlying the Rolling Downs Group is Tertiary in age, and the gullies described by Pool lead into northern tributaries of the Flinders River (Vine 1970).

The 'other fossil' mentioned by Pool is ichthyosaurian (QM F15.987; ?*Platypterygius*), comprising a small piece of jaw with remnants of eight teeth, and a vertebra with pieces of rib. These ichthyosaur fragments do not represent the same animal as QM F15.990: they are much more heavily weathered and darkly stained, and the teeth are labyrinthodont, as is typical for ichthyosaurs. Pool and Berney may have suspected a connection between the two specimens because both were collected from the same gully (though on different occasions) and both included a tooth-bearing fragment of jaw. Berney was an experienced collector of fossil material (Turner & Wade 1986) and Longman ensured that all these specimens were registered separately and promptly on their arrival at the Queensland Museum. Consequently, there is no reason to suppose that QM F15.990 might be heterogeneous or that it might comprise fragments selected from some bigger collection of miscellaneous fossils.

There are no pre-Cretaceous rocks anywhere in the vicinity of Alderley (i.e. on the entire 1 : 250 000 geological map showing Alderley station (Vine 1970)). The nearest Permian rocks are glacial boulder-beds more than 80 km away, and the nearest Triassic rocks are redbeds, at least 100 km away and exposed almost entirely in a different drainage basin (the Burdekin River system (Vine & Paine 1974)). Even if the material described here had originated from those redbeds, and had somehow found its way into the Flinders River, it must have survived transport downstream for more than 100 km. Even then it would still need to have travelled a considerable distance upstream to reach the area of Alderley, which seems a physical impossibility.

The preservation of QM F15.990 matches that of other tetrapod bones in the Rolling Downs Group, indicating that they shared a common diagenetic history. The adherent matrix is typical of the Allaru Formation: it is calcareous, unlike the nearest Permian and Triassic sediments, which are siliceous, ferruginous and carbonaceous. Moreover, it seems unlikely that QM F15.990 could have been reworked from older rocks, as there is not a single reported instance of a reworked or derived fossil anywhere in the prolific fauna of the Allaru and Toolebuc Formations (Dettmann *et al.* 1992; Henderson *et al.* 2000). The only allochthonous elements in those marine formations are stray occurrences of driftwood, gastroliths associated with plesiosaur skeletons, and occasional tetrapod carcasses that floated in (or, in the case of pterosaurs, may have been introduced from the air). There are no coarse clastic layers or sedimentary indicators of currents powerful enough to have exhumed and transported petrified bones as large as those of QM F15.990.

In short, we can find no reason to doubt that QM F15.990 originated from the Rolling Downs Group. It seems quite certainly to be Early Cretaceous in age and was probably introduced into the marine environment by flood-waters that also carried the carcasses of sauropods, ankylosaurs and ornithomimid dinosaurs (Molnar 1991, 1996a,b).

#### (c) Phylogenetic affinities

In practically every aspect of its gross and detailed structure the maxilla is closely matched in a skull of *Dicynodon* sp. from the Permian of South Africa (illustrated by Owen (1876) as *D. pardiceps* and subsequently by Brink (1982–1988), as *D. lacerticeps*). In addition, it bears a strong resemblance to the maxilla in other examples of *Dicynodon* (see, for example, Cluver & King 1983, figs 24, 25) and in many other genera and species of dicynodonts (see, for example, Owen 1845, 1876; Pearson 1924a; Ewer 1961; Cox 1968, 1991; Keyser & Cruickshank 1979; Brink 1982–1988; Cluver & King 1983; King 1990; Renaut & Hancox 2001).

More detailed comparisons are unrewarding for three reasons. First, the Alderley maxilla is rather generalized in its morphology: although it possesses numerous dicynodont features, these are distributed universally or very widely among dicynodonts. Second, there is no consensus on the taxonomy of *Dicynodon* (including '*Daptocephalus*') and other dicynodonts such as *Dinanomodon*, *Odontocyclops*, *Dinodontosaurus* and *Kannemeyeria* (Keyser & Cru-

ickshank 1979; Brink 1982–1988; Cluver & King 1983; Cox 1998; Renaut & Hancox 2001). Third, the maxilla is a poor taxonomic discriminator, being subject to extensive minor variation within individual genera and species (see, for example, Pearson 1924a; Cluver 1971; Cluver & Hotton 1981; Brink 1982–1988). In these circumstances the Alderley specimen may be identified no more precisely than ‘dicynodont’.

However, most (probably all) Triassic dicynodonts are members of a single widely distributed clade, sometimes designated the family Kannemeyeriidae (containing subfamilies Kannemeyeriinae and Lystrosaurinae) or sometimes divided into two sister-families—Kannemeyeriidae (*sensu stricto*) and Lystrosauridae. Regardless of its taxonomic rank, that clade appears to be the sister-group of the Dicynodontidae, which includes the highly speciose genus *Dicynodon* (Cluver & King 1983; Angielczyk 2001; Maisch 2002). The only dicynodont previously reported from Australia is an Early Triassic form which has been likened both to *Lystrosaurus* and to *Kannemeyeria* (King & Thulborn 1983; Thulborn 1983). Consequently, we suspect that the Alderley dicynodont was a late-surviving member of the clade that included *Dicynodon*, *Lystrosaurus* and *Kannemeyeria*. The existence of that clade was inferred by Cluver & Hotton (1981, p. 142), who suspected that it might transpire to be ‘geographically and stratigraphically the most wide-ranging dicynodont taxon’ (see also Rubidge & Sidor 2001). In the conservative proportions of its nasal and maxilla the Alderley dicynodont is more similar to *Dicynodon* and *Kannemeyeria* than to the grotesquely short-snouted *Lystrosaurus* (figure 4).

#### (d) *Unusual anatomical features*

A few features deserve brief discussion because they have a limited or sporadic distribution among the dicynodonts and would not necessarily be expected to occur in a late-surviving form.

The conspicuous pocket in the anterolateral face of the maxilla is a feature of extremely variable occurrence among dicynodonts. In most specimens this pocket is lacking or so shallow as to be overlooked, but in others it is a distinct saucer-like depression. A good example was illustrated by Owen (1876, pl. 38) in a large *Dicynodon* skull, and another was shown by Cox (1965, fig. 14) in a specimen of *Dinodontosaurus*. In its most strongly developed form, as in the Alderley specimen, the maxillary pocket is so deep as to expose the root of the tusk. A nearly identical pocket was illustrated by Camp (1956, fig. 42B) in a left maxilla of the African dicynodont *Kannemeyeria latifrons*, whereas Camp & Welles (1956, fig. 4A) showed an equivalent ‘pit’ in a right maxilla of the North American *Placerias gigas* (see also Cox 1965, fig. 24).

The function of the maxillary pocket is unknown. Camp & Welles (1956) suggested that it might be an old alveolus, perhaps containing a deciduous tusk, but this seems unlikely as dicynodonts did not normally indulge in tooth replacement: they had continuously growing tusks. Moreover, a replacement tooth would be expected to develop on the medial side of the functional tusk, not on its lateral side. It seems more likely that the maxillary pit contained a gland, as both the Alderley maxilla and Owen’s (1876) illustration of *Dicynodon pardiceps* show a shallow groove extending anterodorsally from the maxil-

lary pocket towards the external naris. That arrangement is reminiscent of the glandular pit and secretion-conducting grooves described by Brink (1956) in some examples of the cynodont therapsid *Thrinaxodon*. Despite those conjectures the maxillary pocket remains a poorly understood feature that occurs only sporadically among dicynodonts, seemingly as an individual variation. Although its presence in the Alderley maxilla is unusual, it is far from unprecedented, being rivalled in some examples of *Dicynodon*, *Kannemeyeria*, *Placerias* and other big dicynodonts.

In many dicynodonts the septomaxilla is exposed superficially at the posteroventral margin of the external naris, but in the Alderley specimen this part of the narial rim appears to be formed entirely by the maxilla. However, in bigger Triassic dicynodonts the maxilla often curves over to form the rim of the naris, and the septomaxilla is tucked away internally, without any posteroventral exposure on the surface of the snout. This arrangement is seen, for instance, in the kannemeyeriids illustrated by Renaut & Hancox (2001) and also in some Permian dicynodonts, including examples of *Dicynodon* (see, for example, Cluver & King 1983, fig. 25; King 1990, fig. 1.4). Consequently the maxilla from Alderley would not necessarily be expected to retain a superficial exposure of the septomaxilla if, as we suspect, it represents a late survivor of the clade that includes *Dicynodon* and the Triassic forms *Kannemeyeria* and *Lystrosaurus*.

The presence of a postcanine tooth might also seem unusual, as marginal teeth other than the tusk tended to be lost relatively early in dicynodont history and are frequently lacking in Late Permian and Triassic forms (King 1990; Modesto *et al.* 1999). On initial inspection the Alderley maxilla revealed an irregular patch of dentine-like tissue in the region adjoining the palatine. This tooth-like tissue seemed to be folded into a series of small bumps or tubercles, very like the ‘palatal tubercles’ illustrated by Ewer (1961) in a large skull of *Dicynodon* (*Daptocephalus*). Ewer (1961, pp. 386–387) thought it ‘likely that palatal tubercles may have been present in other species of anomodont, although they have not been recorded’.

The Alderley specimen seemed to bear out Ewer’s suspicion, as it appeared to demonstrate the existence of palatal tubercles, or something very like them, in another big dicynodont. However, careful preparation revealed that the ‘tubercles’ in the Alderley maxilla were actually remnants of a single conical tooth. It is not a replacement for the tusk, which is too far away and continuously growing anyway (i.e. not replaced): either it is an individual aberration, such as a supernumerary tooth, or it is a normal postcanine tooth. As stray ‘extra’ teeth do sometimes occur in dicynodont maxillae (e.g. in *Kannemeyeria*; see Camp (1956, fig. 50B), where it is called a ‘secondary tusk’), an aberrant individual would not be unprecedented. Even so, postcanine teeth do occur in a fair number of dicynodont genera, including *Emydops* (e.g. Crompton & Hotton 1967, fig. 1A), *Tropidostoma* (e.g. Cluver & King 1983, fig. 14A), and even some examples of *Dicynodon* (e.g. Pearson 1924a, p. 810), and recent phylogenetic analysis (Angielczyk 2001) found that some of these scattered occurrences of teeth in higher dicynodonts are likely to represent reversals from a toothless condition. In short, postcanine teeth do occur sporadically

among higher dicynodonts. They are persistent or recurrent primitive features (Crompton & Hotton 1967), and their presence in a Cretaceous dicynodont is no more surprising or significant than the persistence of discrete vertebral intercentra in some extant mammals.

#### (e) *Biogeographical context*

The Cretaceous tetrapod fauna of Australia is already known to include the world's latest-surviving temnospondyl (Warren *et al.* 1991, 1997), along with some seemingly anachronistic or archaic dinosaurs (see Molnar 1980, 1992; Henderson *et al.* 2000), and the presence of a relict dicynodont is further evidence for the existence of a zoogeographic barrier or filter between Australia and the other Gondwana continents. The effects of geographical isolation are detectable in Australia's terrestrial tetrapod fauna as early as the start of the Triassic (Thulborn 1986a), even before Australia and Antarctica had begun to detach from the remainder of Gondwana, and the unexpectedly late survival of a dicynodont implies that such effects persisted, and perhaps intensified, through the Jurassic and Cretaceous.

The discovery of a late-surviving dicynodont parallels the earlier and equally surprising discovery that temnospondyls persisted into the Early Cretaceous in East Gondwana. Before 1977 it was assumed that temnospondyls had suffered extinction in the Late Triassic, along with dicynodonts, but subsequent discoveries extended the history of Australian temnospondyls into the Middle Jurassic (Warren 1977; Warren & Hutchinson 1983) and, eventually, into the Early Cretaceous (Warren *et al.* 1991, 1997). In the interim it was discovered that temnospondyls had also survived into the Middle Jurassic in China (Dong 1985) and into the Late Jurassic in central Asia (Nessov 1988).

Here, it must be borne in mind that Australia has yielded an extremely poor fossil record of Mesozoic tetrapods. Continental vertebrates of Early Triassic age (*ca.* 250 Myr ago) are reasonably well represented in Australia, mainly in the Arcadia Formation of Queensland, the Blina Shale and Kockatea Shale of Western Australia, and the Knocklofty Formation of Tasmania (Thulborn 1986a,b; Molnar 1991; Warren 1991). But between the Early Triassic and the Early Cretaceous there is a huge gap in Australia's fossil record of tetrapods. There are none at all from the Middle and Upper Triassic. A solitary prosauropod dinosaur, *Agrosaurus macgillivrayi*, was long thought to have originated from the Upper Triassic of northeastern Australia (Seeley 1891), but its provenance was uncertain (the specimen was purchased at auction) and it now seems more likely to have been collected in southwestern England. The Jurassic rocks of Australia have yielded only a handful of terrestrial vertebrates: a partial sauropod skeleton (*Rhoetosaurus* (Longman 1926, 1927)), an isolated dinosaurian tail vertebra (Long 1992), a fragment of theropod tibia (*Ozraptor* (Long & Molnar 1998)), a temnospondyl skull with associated postcranial fragments (*Siderops* (Warren & Hutchinson 1983)) and a single piece of temnospondyl jaw (*Austropelor* (Colbert 1967)). Moreover this handful of Jurassic tetrapods is decidedly anomalous: nowhere else on earth does one encounter temnospondyls coexisting with freshwater plesiosaurs, as in the Middle Jurassic Evergreen Formation of Queens-

land (Thulborn & Warren 1980). Against this backdrop of rare and anachronistic tetrapods the occurrence of a late-surviving dicynodont may not seem so surprising after all.

Palaeogeographic reconstructions of Australia in the Middle and Late Albian (figure 1c) indicate that the Alderley dicynodont inhabited a very remote corner of Gondwana. Its remains probably entered the epicontinental sea of the Eromanga Basin in the form of a stray carcass washed in from an adjoining land area. The nearest terrestrial source is to the east, on the margin of the Queensland Plateau, which was separated from the remainder of the Australian and Antarctic landmass by a seaway during the Aptian marine transgression. Even during phases of marine regression the Queensland Plateau would have lain at the extremity of an enormous East Gondwana peninsula and would have maintained only a tenuous trans-Antarctic connection to the other Gondwana continents (figure 1b).

Evidently some members of the longest-surviving dicynodont clade persisted until the Early Cretaceous in an Australian refugium that was only distantly and intermittently connected with the remainder of Gondwana. Those isolated dicynodonts were probably rare animals, by comparison with the herbivorous dinosaurs that flourished over the greater part of Gondwana, and there would be little likelihood of encountering them in the fossil record, and particularly when the record is so incomplete as that of Australia.

Presumably dicynodonts inhabited some part(s) of East Gondwana continuously from the Early Triassic to the Early Cretaceous. That immense interval of time witnessed profound changes in the composition of Gondwana floras (Wright *et al.* 2000), implying that the herbivorous dicynodonts must have been sufficiently versatile to have survived substantial changes in the composition of their diet. In the Australian region late-surviving dicynodonts would have coexisted with all the major groups of dinosaurs—theropods, ornithischians and sauropodomorphs. Elsewhere in the world every large terrestrial tetrapod of Jurassic and Cretaceous age was a dinosaur, but in Australia large terrestrial tetrapods were sometimes dicynodonts, not dinosaurs. As numerous and well-studied vertebrate faunas of Early Cretaceous age in Eurasia, Africa and the Americas (Molnar 1980, 1992; Weishampel 1990) have yielded no evidence of dicynodonts, it seems that Australia's tetrapod fauna may have been as distinctive and anachronistic in the Mesozoic as it is at the present day.

Dicynodonts probably resembled pigs, hippopotamuses or rhinoceroses in some aspects of their appearance and behaviour, though they have no very exact counterparts among living mammals. They do, however, show striking convergences with the ceratopians or 'horned dinosaurs' of the Cretaceous (Camp & Welles 1956; Chrulow 1976; Cox 1991): both were robust large-headed quadrupeds, with a horny beak at the front of upper and lower jaws, a greatly expanded temporal region, a powerful shearing jaw-mechanism, sprawling forelimbs, erect hindlimbs and an expanded ilium correlated with a shortened tail. Thus, in general terms at least, the late-surviving dicynodonts of Australia might be regarded as autecological equivalents of the ceratopians in Cretaceous dinosaur faunas of Asia and North America.



We thank Joanne Wilkinson (Queensland Museum) for bringing Longman's material to our attention, Victoria Harrison for assistance with the Queensland Museum Library archives, Morag Wilson (Veterinary Science Clinic, University of Queensland) for radiographic work, Carole Burrow (Zoology and Entomology, University of Queensland) for help in preparing the figures, and an anonymous referee for some helpful and constructive comments.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.